Deep macroevolutionary impact of humans on New Zealand's unique avifauna

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Highlights

- Large numbers of bird species went extinct in New Zealand after human colonization
- We reconstruct diversity dynamics of New Zealand's birds
- It would take 50 million years (Ma) to recover the diversity of bird species lost
- If threatened species go extinct, up to 10 Ma needed to return to today's levels

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In Brief

New Zealand was home to a unique bird fauna when humans arrived. Today, many of its evolutionary isolated lineages are endangered or extinct. Valente et al. reconstruct the natural macroevolutionary dynamics of birds in New Zealand and find that 50 million years would be needed for bird species diversity to return to pre-human levels.

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Deep Macroevolutionary Impact of Humans on New Zealand's Unique Avifauna

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SUMMARY

Islands are at the frontline of the anthropogenic extinction crisis [1]. A vast number of island birds have gone extinct since human colonization [2], and an important proportion is currently threatened with extinction [3]. While the number of lost or threatened avian species has often been quantified [4], the macroevolutionary consequences of human impact on island biodiversity have rarely been measured [5]. Here, we estimate the amount of evolutionary time that has been lost or is under threat due to anthropogenic activity in a classic example, New Zealand. Half of its bird taxa have gone extinct since humans arrived [6, 7] and many are threatened [8], including lineages forming highly distinct branches in the avian tree of life [9–11]. Using paleontological and ancient DNA information, we compiled a dated phylogenetic dataset for New Zealand's terrestrial avifauna. We extend the method DAISIE developed for island biogeography [12] to allow for the fact that many of New Zealand's birds are evolutionarily isolated and use it to estimate natural rates of speciation, extinction, and colonization. Simulating under a range of human-induced extinction scenarios, we find that it would take approximately 50 million years (Ma) to recover the number of species lost since human colonization of New Zealand and up to 10 Ma to return to today's species numbers if currently threatened species go extinct. This study puts into macroevolutionary perspective the impact of humans in an isolated fauna and reveals how conservation decisions we take today will have repercussions for millions of years.

RESULTS

New Zealand's biota is known for its evolutionary distinctiveness and unusual species composition [6, 13–15]. Despite its origins as an ancient continental fragment, New Zealand has a distinctively insular character, leading Alfred Russel Wallace to declare that its "wonderfully isolated" biota resembles that of oceanic islands [14]. A remarkable feature of New Zealand is that, unlike other large landmasses, its vertebrate fauna has long been dominated by birds, many of which form highly distinct evolutionary lineages [9, 10, 16]. The Quaternary avifauna of New Zealand—often called a "land of birds"—includes examples such as a giant nocturnal parrot (kakapo), the flightless moa (Dinornithiformes), and the country's national bird, the kiwi (Apterygidae) [6]. A characteristic feature of New Zealand is the taxonomic and ecological uniqueness of its bird clades, generally attributed to its prolonged geographical isolation and/or ancient Gondwanan heritage [16–18]. Compared to other similar-sized landmasses, there are relatively few species of land (non-aquatic) birds, most of which are found nowhere else [6]. The country harbors several groups forming deep isolated phylogenetic branches [9], including the sister clade of parrots (Strigopoidea) [19] and passerines (New Zealand wrens, Acanthisittidae) [9, 20], and two endemic clades of palaeognaths (kiwi and moa), the sister group to all other birds [10].

The unique avifauna of New Zealand is an excellent example to study the role of human occupancy in disturbing natural communities [21]. New Zealand was the last major habitable land area to be settled by humans [22]. Polynesian Maori arrived about 700 years ago and Europeans have been present for 200–300 years [23, 24]. Although all bird species known from Late Pleistocene deposits survived into the period of first human occupation, nearly half were driven to extinction during the following years of settlement [7, 25]. The avifauna of New Zealand suffered one of the largest waves of extinction documented. The high incidence of flightlessness (over a third of land bird species upon human arrival), large body size, and behavioral naiveté have contributed toward susceptibility of native birds to hunting, introduced species and land-use change [7, 26]—a recurring pattern in most isolated islands worldwide [1, 2, 4]. Despite innovative conservation efforts in the country over the last 50 years, over 30% of extant species remain threatened with extinction, and nearly two thirds could be under threat in the future [8].

While the impact of humans on New Zealand's extinct and threatened bird species numbers is relatively well understood, little is known about the long-term macroevolutionary impact of anthropogenic extinction. In other words, how far have humans perturbed this unique and isolated biological assembly

Table 1. Sources of Published Trees Including Information on Dating Methods Used in the Original Publications

Taxonomic Group	Source of Dated Tree	Calibration	Notes
Acanthisittidae	[16]	fossils	Figure 1 from Mitchell et al. [16]; Palaeocene maximum; *Kuiornis* constraint
Apterygidae (Kiwi)	[11]	fossils & biogeographical	branching times from [11] and maximum colonization time from [10]
Aptornis	[28]	fossils	
Anseriformes	[29]	secondary	
Callaeidae, Notiomystidae, *Turnagra*	[9]	secondary	
Circus	[30]	molecular rate	
Corvides (*Mohoua*, *Rhipidura*)	[31]	fossils	
Corvus antipodum	[32]	fossils	
Coturnix	[33]	secondary	
Dinornithiformes (Moa)	[34]	fossils & time-stamped data	branching times from [34] and maximum colonization time from [10]
Falco	[35]	fossils	two options, chose older age
Meliphagidae (*Anthornis Prosthemadera Gerygone*)	[36]	fossils & secondary	
Poodytes	[37]	molecular rate	
Porphyrio	[38]	secondary	
Raillidae	[39]	secondary	
Todiramphus sanctus	[40]	molecular rate	

See also Table S1 and Data S1 and S2.

from its natural state? And how deep will the evolutionary impact be if currently threatened species go extinct? Would diversity quickly return to natural levels if left to evolve under its natural trajectory of colonization and speciation (with no further human-induced extinctions)? Here, we address these questions for the first time in an insular avifauna.

We compiled the first complete dated molecular phylogenetic dataset of New Zealand's native resident land birds—comprising dozens of extant and extinct colonist lineages (Data S1 and S2). A previous study [27] produced a complete phylogeny for the New Zealand avifauna, by adding 112 taxa for which no molecular data was available to pre-assigned locations on the tree, and that phylogeny was not dated. Since that study, many more DNA sequences have been published for a variety of extant and extinct New Zealand species. We use the best available molecular datasets for each group, each of which was dated in a separate phylogenetic divergence dating analysis (Tables 1 and 2). This allows us to include the vast majority of species based on their own molecular data, often from multiple individuals from New Zealand populations. We excluded marine, migratory, vagrant, and introduced species (see STAR Methods). In our main analyses, we include only bird orders for which all or the majority of species are land dwelling (non-aquatic), and we term this the "main dataset." We also repeated analyses including Anseriformes (ducks, geese, and swans), which includes some land-dwelling taxa. The phylogenies of the main dataset revealed 39 separate avian colonizations of New Zealand and 11 *in situ* "radiations" consisting of two or more descendant species present upon human arrival, the largest being the moa (nine species) and the acanthisittid wrens (seven species), as summarized in Table S1 and Figure 1. Most colonizations took place less than 15 million years ago (mya). In total, 30 species of our focal group have gone extinct since humans arrived, spread across 15 colonist lineages, 12 of which lost all of their descendant species. We account for all 30 extinct species in the analyses, not only for the 23 whose genetic material has been sequenced using ancient DNA methodologies [52] but also for the remaining 7 species that we treat as missing, which means that their existence still contributes to our inference.

We used the DAISIE (Dynamic Assembly of Islands through Speciation, Immigration, and Extinction) [12] framework to estimate pre-human (i.e., natural) rates of species accumulation in New Zealand. Its maximum likelihood implementation allows parameters of colonization, speciation via cladogenesis (i.e., when one species splits into two new species) and anagenesis (i.e., when a new species is formed without lineage splitting) and natural extinction to be estimated based on the colonization and branching times for an entire community on an insular system. DAISIE has been shown to estimate these rates with little bias [53]. The rate of natural extinction—i.e., the background rate at which species go extinct from the system in the absence of humans—is usually well estimated in this framework [53, 54]. The method uses information from the distribution of branching times within island radiations in combination with additional information from the separate colonization times. In its parameterization of extinction, DAISIE assumes and accounts for the fact that there may have been several lineages of taxa that were present on the island before humans but which went completely extinct due to natural causes, leaving no extant descendants (and often, no fossils). We did not test for non-homogeneous rates of colonization, speciation, and extinction (e.g., as in [12]) because we do not have an *a priori* hypothesis

Table 2. Information on Alignments Compiled for This Study and Used for New Divergence Dating Analyses

Taxonomic Group	Molecular Marker	Main Source of New Zealand Sequences	Rate Used	Rate Reference	Model
Aegotheles	CytB	[41]	0.01105	[42]	HKY+G
Anthus	CytB	[9]	0.01035	[42]	HKY+I+G
Harpagornis	CytB	[43]	0.00905	[42]	HKY+I+G
Hemiphaga	CytB	[44]	0.0098	[42]	GTR+I+G
Ninox, *Sceloglaux* (owls)	ND2	[45, 46]	0.016	[47]	HKY+G
Petroica	CytB	[48]	0.01035	[42]	HKY+G
Psittaciformes	CytB	various	0.0075	[49]	HKY+I+G

See also Table S1 and Data S1 and S2.

of different rates for a specific group and because we are interested in average rates in New Zealand.

We extended DAISIE to accommodate that most New Zealand bird radiations are very old and have no extant close relatives. The method was extended by allowing for a colonization event to have occurred any time between the stem age and the crown age of a New Zealand radiation (see STAR Methods). We implemented the new method in a new version of the R package DAISIE. We then fitted several DAISIE models to the phylogenetic data, assuming that New Zealand has existed as a continuously habitable isolated insular system for the past 52 Ma (but see STAR Methods for a sensitivity analysis of this assumption). Under the best supported macroevolutionary model of bird species accumulation in New Zealand (model M1, Table S2), bird species colonized at a rate of 4.7 events every million years (Ma), while new species originated through both cladogenesis and anagenesis at a rate of 0.125 and 0.33 speciation events per lineage per Ma, respectively, and went extinct through natural extinction at a rate of 0.19 extinction events per Ma. Because extinction exceeds the rate of cladogenesis, avian biodiversity on New Zealand is maintained by colonization; i.e., New Zealand constitutes a macroevolutionary sink for birds. Simulations of the model reveal a good fit to the data (Figure S1).

We estimated how long it would take on average for bird species diversity in New Zealand to return to a given level using a recently developed island evolutionary return time metric [54]. This metric uses the information on the natural rates of species assembly for a given insular system (estimated using DAISIE) and measures how long it would take for species diversity on that island to increase to a predetermined level (often pre-human levels) by simulating under those same rates into the future. This metric is calculated for each island system (e.g., island, lake, archipelago) and is thus island rather than lineage centric and can allow for the macroevolutionary impact of humans on different islands to be compared. The evolutionary return time differs from methods that measure the amount of lost phylogenetic diversity [55] because the latter approaches do not take into account the specific local biogeographical processes that are taking place on each island (and which differ with island characteristics such as area and isolation [56]). We studied three scenarios: (1) the return from current diversity to pre-human and pre-European number of species; (2) the return from diversity that would remain if currently threatened species (critically endangered, endangered, and vulnerable) became extinct back to current number of species; (3) the return from diversity that would remain if currently threatened as well as near-threatened species became extinct back to the current number of species.

The island evolutionary return time metric results for the main dataset show that it would take approximately 50 Ma for total species diversity in New Zealand to return to pre-human levels and nearly 4 Ma to return to pre-European levels (Table 3; Figure 1 for total species; Figure S2 and Quantification and Statistical Analysis for endemic and non-endemic species). The return time from present to pre-European diversity is much shorter than the return time from pre-European to pre-Human diversity because of the large differences in the number of species separating each state (six species difference for the former, 22 species difference for the latter). We further found it would take nearly 6 Ma to return to today's diversity if all 13 currently threatened New Zealand terrestrial bird taxa go extinct, including the charismatic kakapo and several species of kiwi. We also considered an even more pessimistic scenario where species that may become threatened in the future also go extinct, for example, species that have experienced significant declines in recent years, or that depend on conservation efforts to remain out of danger, such as the North Island kōkako or the South Island saddleback. In this scenario, up to 10 Ma would be needed to restore diversity to today's levels. If we include ducks, geese, and swans in the analyses, we find slightly shorter evolutionary return times (40 Ma to return to pre-human diversity, Table S3), because the estimated rates of colonization are higher for the dataset including Anseriformes. Note that return times are calculated for the avifauna as a whole and constitute averages, and thus our results may be compared with future studies that may arise using this metric.

DISCUSSION

Our analyses reveal that in addition to its impact on global avian diversity, anthropogenic activities on islands have also led to a huge loss of evolutionary history. The island evolutionary return time metric shows that it would take 50 Ma of bird evolution to build up the diversity that has been wiped out from New Zealand in the last 700 years, 4 Ma to recover the diversity lost in the less than 250 years since Europeans arrived, and up to 10 Ma to recover the diversity that is currently under threat (Table 3; Figure 1). In comparison, the only other study to measure the evolutionary impact of humans on an island system found that "only" 8 Ma have been lost in Caribbean bats [54]. Our evolutionary return time estimates for New Zealand also exceed previous estimates for mass-extinction rebounds in typical biodiversity communities

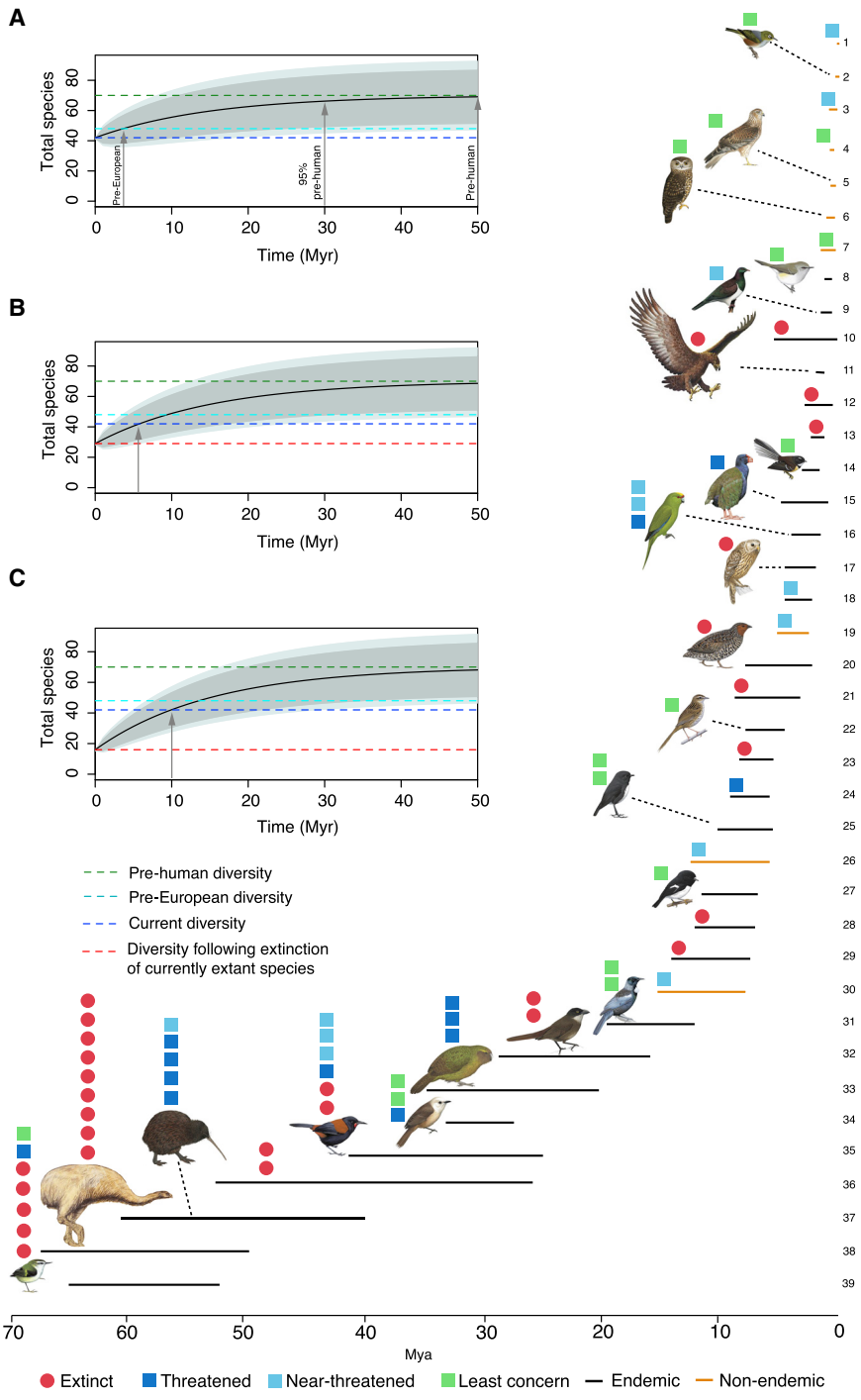

Figure 1. Colonization Times and Evolutionary Return Times for Total Number of Species

(A–C) Colonization times based on Bayesian divergence dating analyses (95% highest posterior density interval). Colored symbols above colonization times represent all species present upon human arrival and that descended from that colonization event. Numbers indicate clades in Table S1. Plots show expected future bird diversity in New Zealand for a range of scenarios: (A) return time from current to pre-human diversity; (B) return time if threatened species go extinct; (C) if threatened and near-threatened species go extinct. Gray arrows indicate evolutionary return times. Data based on the M1 model. Shaded areas show the 2.5–97.5 (light) and the 25–75 (dark) percentiles. Birds drawings were used with permission from del Hoyo et al. [50]. Haast's eagle (11) by John Megahan used with his permission. Moa image (38) courtesy of Colin Edgerley, Richard Holdaway, and Trevor Worthy [51].
See also Figures S1 and S2.

based on the fossil record (5–10 Ma [57]). In this study, we have focused on the land bird fauna, but anthropogenic extinctions and threatened species in New Zealand are not restricted to this group. We did not include shorebirds and seabirds as their biogeography should be modeled using a different model than DAISIE, but they constitute a significant proportion of the avifauna (66 species, plus many more on offshore islands). Given that they include multiple endemics (14 species), of which several species are endangered nationally [8] and that they have also experienced extinctions after human arrival (at least four species in our focal geographical area), they would likely lead to similar evolutionary return times reported here.

It is important to know how much evolutionary time has been lost or may be lost, even though we already know how many species went extinct or are threatened [55, 58]. The island evolutionary return time metric provides a new perspective on the profound impact humans have on biodiversity and on the avian tree of life. Furthermore, we hope the measure of future potential evolutionary time lost may help promote and guide conservation efforts in some of the world's most unique biological assemblies. It is often argued that, if left alone, nature will eventually return to its original diversity (even though the exact same species will not re-evolve). In fact, if we consider the number of bird species that have been introduced to New Zealand (37 species from 16 different families [8]), it could be claimed diversity has already achieved pre-human levels (as may have been the case in other remote islands worldwide [59]). However, the high diversity of introduced species obscures the fact that the native bird species of New Zealand have been under immense pressure, and introduced species should not have an equivalent value for biodiversity indices if one aims to protect natural processes. Our study thus clearly reveals that the recovery of New Zealand's diversity will not be quick and will, for example, far exceed the amount of time that humans have existed. As conservation funds are limited, measuring the evolutionary time under

Table 3. Diversity Metrics of Native Breeding Terrestrial New Zealand Birds Belonging to Our Focal Group

Species Lost/Under Threat	Total	Endemic	Non-endemic
Extinct since humans arrived	30	30	0
Extinct since Europeans arrived	8	8	0
Threatened	13	13	0
Near-threatened	13 (12)	8	5 (4)
Diversity Present at Different Stages	**Total**	**Endemic**	**Non-endemic**
Pre-human diversity	70	62	8
Pre-European diversity	48	40	8
Current diversity	42 (40)	32	10 (8)
Diversity excluding threatened	29 (27)	19	10 (8)
Diversity excluding threatened and near threatened	16 (15)	11	5 (4)
Average Island Evolutionary Return Time for Total Species (Ma)	**Total**	**95% of Total**	
Return to pre-human diversity	50 (>50)	30 (38)	
Return to pre-European diversity	3.6 (5.4)	2 (3.5)	
Return to current diversity if threatened go extinct	5.75 (6.3)	4.5 (4.9)	
Return to current diversity if threatened and near-threatened go extinct	10 (10.7)	9.1 (9.3)	

Main dataset, excluding Anseriformes. Metrics for different stages and under different extinction scenarios. Numbers in brackets correspond to the analyses excluding *Fulica atra* and *Zosterops lateralis*, which colonized naturally after humans were already present. See also Tables S2 and S3.

threat in multiple islands worldwide may contribute to conservation efforts by prioritizing the preservation of islands that currently have the most evolutionary history under threat. We hope this approach may help guide future prioritization attempts and aid in decision making—for example, by helping choose which islands should be targeted for eradication of invasive species [60]. Regardless of the path we choose, our results caution that the policy decisions we make today will have implications far into the future. Luckily, New Zealand's pioneering bird conservation efforts may yet prevent millions of years of evolutionary history from further being lost.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.06.058.

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AUTHOR CONTRIBUTIONS

L.V. and J.C.G.-R. designed the study, collected the data, and wrote the manuscript. R.S.E. provided theoretical input and developed analytic tools. L.V. performed the analyses. All authors read and commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
BEAST trees (posterior distribution and maximum clade credibility trees).	This study	https://doi.org/10.17632/wj3xrjmj28.1.
DAISIE R objects containing the dataset with the times of colonization and speciation used for the maximum likelihood analyses.	This study	https://doi.org/10.17632/5p3zf4wf3r.1.
Software and Algorithms		
DAISIE R package 1.5	This study and [12]	https://github.com/rsetienne/DAISIE
BEAST 2	[61]	www.beast2.org
jModeltest 2.1.5	[62]	https://github.com/ddarriba/jmodeltest2

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests should be directed to and will be fulfilled by the Lead Contact, Luis Valente (luis.valente@naturalis.nl). This study did not generate new unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Geographical unit and taxon selection

Our focal geographical unit comprises the large North and South Islands and their offshore and adjacent islands, such as Great Barrier, Stewart, Solander and Three Kings (hereafter New Zealand). We exclude outlying islands (Antipodes, Auckland, Bounty, Campbell, Chatham, Kermadec and the Snares) as these are sufficiently isolated to constitute independent macroevolutionary biogeographical units for birds.

We compiled a complete taxon list of the New Zealand avifauna present on first human contact approximately 700 years ago, based on recent checklists [25, 63]. We exclude marine, migratory, vagrant and introduced species. Although there are many endemic, extinct and/or endangered aquatic species of birds in New Zealand [6], we chose to exclude these in order to compare species with a largely land-dwelling ecology, because we fit models with diversity-dependence that assume species competition for niches. DAISIE assumes a common mainland pool for each clade, so a bird order cannot be partially included. In other words, if a bird order that is largely terrestrial includes one aquatic species, we cannot exclude the aquatic species, we must either include the whole order or exclude it entirely. For this reason we chose to include bird orders whose majority of species in New Zealand are terrestrial. Therefore we include Gruiformes (rails), even though some of their species are aquatic (e.g., coot). Likewise, we excluded from the main analyses orders whose species are mostly aquatic, including Anseriformes (ducks, geese and swans), which includes some semi-terrestrial species. Thus, in our main analyses ('main dataset') we include: Apodiformes, Apterygiformes, Columbiformes, Coraciiformes, Dinornithiformes, Falconiformes, Galliformes, Gruiformes, Passeriformes, Psittaciformes, Strigiformes; that is, all the orders with mainly terrestrial species (mostly 100% terrestrial in New Zealand, except Coraciiformes and Gruiformes). In order to assess how the inclusion of Anseriformes - a group which includes some semi-terrestrial species - would affect our results, we also ran an analysis including this order. There were 15 species of Anseriformes in New Zealand upon human arrival, eight of which have gone extinct. We include this analysis only as Supplemental material (Data S3; Tables S2 and S3) because: a) the great majority of species of Anseriformes in New Zealand are aquatic; b) phylogenetic data for this group is very poor compared to other groups – only one out of the eight extinct taxa have been sequenced. We provide the data used for the analyses including Anseriformes in Data S3.

We followed the *Handbook of the Birds of the World* [50] (HBW) for nomenclature and species delimitations. For a few cases, the nomenclature of HBW differs from that used in the checklist of the Ornithological Society of New Zealand [63], and we indicate all those cases in Data S1. Our main dataset includes 72 species, and the dataset with Anseriformes includes 87 species.

Extinct species

We treat extinct and extirpated taxa that went extinct because of humans as though they had survived until the present, following the approach of Valente et al. [54]. We identified anthropogenic extinctions based on published [63] and online data [64]. Our main dataset includes 30 taxa that have gone extinct since human arrival (Data S1). Of these, at least 23 have previously been sequenced using

ancient DNA [52]. Sequences were not available on GenBank for the remaining seven extinct taxa. Three of these belong to endemic New Zealand radiations and we added them as unsampled species to the designated clade (Acanthisittidae (added *Dendroscansor decurvirostris* and *Pachyplichas jagmi*) and *Turnagra* (added *Turnagra tanagra*)). The remaining four species (*Capellirallus karamu*, *Circus teauteensis, Fulica prisca*, and *Tribonyx hodgenorum*) are extinct species which constitute independent colonizations and we included them by assuming that they could have colonized any time since the origin of the genus they belong to and the present (Data S1). Hence, all 30 extinct species are accounted for in our approach. For the sensitivity analyses including Anseriformes, there are eight additional extinct species, but molecular data is only available for one species (*Cygnus sumnerensis)* (Data S3).

Sampling for phylogenetic analyses

For each bird species, we sampled individuals from New Zealand as well as from the taxon's closest relatives outside our geographical unit. If the taxon was a species endemic to New Zealand, we aimed to sample multiple individuals from that species, as well as from the most closely related species according to available phylogenetic data. If the taxon was not endemic, we sampled individuals from New Zealand population(s) as well as populations of the species from nearby landmasses (mostly New Zealand's outlying islands, Australia, Lord Howe, New Caledonia and/or Norfolk Island).

Endemicity status is one type of data that DAISIE uses to estimate speciation rates. We consider endemic to New Zealand species with populations only in our focal geographical unit as defined above. For six species (*Anthornis melanura*, *Cyanoramphus novaezelandiae*, *Petroica macrocephala*, *Prosthemadera novaeseelandiae*, *Rhipidura fuliginosa*, *Sceloglaux albifacies*) found exclusively in our focal geographical unit plus a few outlying islands, we assume that the speciation events that originated them took place in New Zealand and that they later colonized the outlying islands, and thus classified them as endemic for the purposes of the DAISIE analyses (otherwise, rates of speciation within New Zealand would be underestimated).

Age of New Zealand and Oligocene "drowning" event

The geological history of New Zealand and the possibility of establishment of species via vicariance or overwater dispersal have been the subject of considerable debate [17, 18, 65, 66]. The Zealandia sub-continent started to break away from Australia and Antarctica 82 million years ago (Ma), but full separation from Australia is believed to have occurred only later, approximately 55–52 Ma [67, 68]. The hypothesis that New Zealand was entirely submerged in the Oligocene 25–22 Ma [69] has now been deemed unlikely. Current consensus is that at least part of New Zealand landmass remained available to sustain terrestrial avifauna during the late Oligocene [15, 17], with a recent review of phylogenetic data finding no evidence for a deficit of pre-Oligocene lineages in New Zealand [15]. While most of the colonizations in our dataset postdate this event, seven are older and appear to have survived it, and we note that turnover may lead to an apparent increase of colonizations toward the present (e.g., extinction and recent colonizations erasing the signature of past colonizations that may have survived the event). To examine whether this period may have significantly affected rates of biota assembly, we fitted a set of DAISIE models (Etienne and Hauffe, pers. comm) where we allow for a shift in rates to take place at 25-22 Ma (the time of the Oligocene event). We allowed for shifts in colonization, cladogenesis and extinction rates during that period. We found that models with a shift (non-constant rates) are not preferred, and that our constant-rates model (M1 model) is favored. Thus our estimates of evolutionary return times are robust to this event. In any case, we stress that we are interested in average rates throughout the entire history of New Zealand.

In our analyses, we assume New Zealand has existed as a continuously habitable isolated insular system for the last 52 Ma. While we cannot completely rule out that three of the groups in our dataset (acanthisittid wrens, kiwi and moa) arrived in New Zealand via vicariance (i.e., before separation from Australia), as the estimated upper bound of their stem age is older than 52 Ma (Table S1; Data S2), we believe it is much more likely that these groups arrived later via overwater dispersal because: a) these three clades are found on very long branches in the phylogenies and it is very likely that an extinct sister group from the ancestral area, which would render a younger stem age and a later inferred colonization age of New Zealand, has not been sampled (e.g., has left no fossils); b) the crown ages of the three groups are much younger than 52 Ma (e.g., younger than 7 Myr in kiwi [11]); and c) recent results in the phylogenetic literature have increasingly shed doubt on the hypothesis of a vicariant origin for these three clades [9, 10, 16, 18]. We also re-ran analyses assuming the much older age of 82 Ma – which would be compatible with an older origin of those groups - and the results on diversification rates and evolutionary return were quantitatively and qualitatively very similar (Table S2), so we do not discuss them in the main text.

METHOD DETAILS

Colonization and speciation times

We obtained times of colonization and speciation for each taxon from three sources: 1) published dated trees; 2) new divergence dated analyses conducted for this study; and 3) historical records of colonization. For 1) and 2), alignments/phylogenies focus mostly on a single genus (e.g., *Aegotheles* or *Petroica*) or radiation (e.g., kiwi or moa), while others include multiple closely related genera or higher order clades (family, order) depending on the diversity and level of sampling of the relevant group. For example, species from the avian infraorder Meliphagides (New Zealand representatives within genera *Anthornis, Prosthemadera* and *Gerygone*) were previously analyzed together in a phylogenetic dating analysis by Marki et al. [36], and we thus include them in the same tree. The nodes in the dated trees used to obtain the estimates of colonization and branching times are given in detail for each taxon in Data S1 and

Data S3. The confidence intervals for colonization and branching times are generally broad (Data S2), reflecting the uncertainty in calibrations and molecular rates, and the use of conservative priors.

For 16 groups (Table 1), well-sampled and rigorously-dated phylogenies were available from recent publications, all of which conducted phylogenetic divergence dating using a variety of calibration methods. We obtained maximum clade credibility trees from online repositories or directly from the authors of these studies – the references for these studies are all given in Table 1. Phylogenetic trees were based on a variety of markers, according to which markers had been mostly sequenced for a given group. For the two New Zealand palaeognath groups (kiwi and moa) branching times for the speciation events of the radiations were available from in-depth publications [11, 34]. However, these publications focused on the radiation within New Zealand rather than the divergence from the outgroup, which is needed for a reliable estimate of the colonization time. So we decided to use the stem age of kiwi and moa obtained from the wider palaeognath phylogeny of Mitchell et al. [10] as the earliest possible colonization time.

For seven groups, we conducted new dating analyses using mitochondrial sequences (CytB or ND2) downloaded from GenBank (n = 664 sequences). We performed phylogenetic divergence dating analyses in BEAST 2 [61], using the substitution model selected in jModeltest [62] (Table 2). For dating these seven groups, we used rates of evolution estimated in avian mitochondrial sequences, which have been shown to evolve in a clock-like fashion at an average rate of ~2% per Ma [42]. Applying average molecular rate calibrations across multiple clades is controversial and can be problematic for ancient clades, due to high levels of heterotachy in birds [70]. We only applied molecular rate dating to extract node ages for branching events at the tips of the trees, for species within genera (e.g., *Hemiphaga*) or populations within species (*Ninox novaeseelandiae*). The only exception was the stem node of Strigopoidea (*Nestor*/*Strigops*, Table 2) which is a deep node in the tree. However, our estimate for this node (20.62 - 35.58 Ma, 95% HPD) is similar to that from a wide fossil-calibrated avian dating analysis (approx. 18 - 48 Ma for the same node) [20].

We obtained rates from the literature using taxon- and marker-specific rates for each group (Table 2). We applied a Bayesian uncorrelated lognormal relaxed clock model, and, for each of the seven alignments ran two independent chains of between 10 and 40 million generations, with a birth-death tree prior. We assessed convergence of chains and appropriate burn-ins with Tracer, combined runs using LogCombiner, and produced maximum clade credibility trees with mean node heights in Tree Annotator. GenBank numbers and BEAST trees for the new dating analyses conducted for this study are given in Mendeley Data. The new molecular alignments used to produce these trees are given in Mendeley Data.

For two taxa – *Zosterops lateralis* and *Fulica atra* – detailed historical records of natural colonization of New Zealand are available. Both are very recent arrivals: the silvereye (*Z. lateralis*) established on the islands in 1856 [71], and the coot (*F. atra*) in 1958 [72]. These species have repeatedly colonized islands in the southwest Pacific from Australia without human intervention [18, 73]. We repeated analyses with and without these species (see 'Island evolutionary return time' section below).

QUANTIFICATION AND STATISTICAL ANALYSIS

Estimating macroevolutionary rates of colonization, speciation and extinction

DAISIE can estimate rates of colonization, natural extinction, cladogenesis and anagenesis with good precision and little bias [53]. It can also estimate a lineage-specific carrying capacity (i.e., the maximum number of species each colonist lineage can attain) under a model of diversity-dependence where rates of cladogenesis and colonization decline with increasing number of species in the colonizing clade.

We extended the DAISIE method to account for the fact that most New Zealand bird radiations are very old and have no extant close relatives. As a result, these radiations tend to be found on very long branches separating the stem age from the crown age (the first branching event within the radiation) of the group. The original DAISIE implementation used the stem age as the precise colonization time, but in the case of New Zealand's ancient radiations subtended by long branches it is very likely that such an age would be a great overestimate due to extinct close relatives that occurred outside of New Zealand not being sampled (e.g., no fossils exist). We thus extended the method to allow for the colonization to have occurred any time between the stem age and the crown age of the radiation. The clades to which this methodology was applied are indicated in Table S1. We implemented the method in a new version of R package DAISIE.

We compared four different DAISIE models: M1 – a diversity-independent model with no carrying-capacity (4 parameters: colonization, cladogenesis, extinction and anagenesis); M2 – like M1 but without anagenesis (3 parameters; all endemic species come from cladogenetic events, species showing an anagenetic pattern are the product of cladogenesis plus extinction); M3 – a diversity-dependent version of M1, with an additional parameter for the per-clade carrying capacity (5 parameters); M4 – like M3 but without anagenesis (diversity-dependent version of M2, 4 parameters). Note that while anagenesis does not increase diversity on the island, it does affect the number of endemics, and the information on numbers of endemics and non-endemics is used for the evolutionary return time calculations. We repeated analyses assuming an age of 52 and 82 Ma. We used a mainland pool of 1000 species, with the assumption that species could have colonized from any landmass in the Pacific region that harbored bird species during the last several Myr (lower pool sizes alter only the per lineage rate of colonization [12]). The datasets used in DAISIE were deposited in Mendeley Data.

We fitted each model using 20 initial sets of randomly chosen starting parameters to avoid being trapped in local likelihood suboptima. We ran a second round of optimisations for each analysis using the estimated ML parameters of the previous run. Models

were compared using the Bayesian information criterion (BIC). To assess goodness-of-fit of the model to the empirical data, we simulated 5,000 datasets with the preferred model and compared the distribution of simulated diversity metrics to those in the real data (Figure S1).

Island evolutionary return time

The island evolutionary return time metric [54] estimates the number of species expected to be present on the insular system at a certain time in the future assuming a given macroevolutionary model, in this case, the M1 model, and a given starting diversity. We counted the number of species that were present upon human arrival (pre-human diversity) and upon European arrival (pre-European diversity) based on reviews of the fossil record [63, 64].

We also counted the number of species that will remain if currently threatened species and near-threatened species go extinct. We extracted threat category for all taxa (Data S1; Data S3) from published assessments. For endemic species, we used the classification of IUCN for the entire species [3]. For non-endemic species IUCN categories do not offer sufficient detail at the New Zealand level, and we used the classification of the Department of Conservation (DOC) of the Government of New Zealand [8] with respect to the status of the species within New Zealand. We translated the DOC categories to IUCN categories in the following way: "At risk" = "Near threatened"; "Not threatened" = "Least concern."

We estimated expected future diversity under the following scenarios (Tables 3 and S3): 1) the return from current diversity to pre-human and pre-European diversity; 2) the return from diversity that will remain if currently threatened species (critically endangered, endangered and vulnerable) go extinct back to current diversity; 3) the return from diversity that will remain if currently threatened plus near-threatened species go extinct back to the current diversity.

Because there have been two natural colonizations since humans have arrived (*Fulica atra* and *Zosterops lateralis*, see above) the extant native non-endemic diversity is actually higher than pre-human non-endemic diversity by two species. We repeated the DAISIE maximum likelihood analyses and island evolutionary return time analyses excluding these two species to take into account the possibility that their colonization may have been favored by human presence. We found that if we exclude these two species the island evolutionary return times would be even higher (Table 3).

Evolutionary return times for endemic and non-endemic species

For endemic species (Figure S2), it would take approximately 45 Myr to return to pre-human levels. If extant endemic threatened species go extinct, it would take nearly five Myr to return to today's diversity. If both threatened and near-threatened endemic species go extinct, more than eight Myr would be needed to recover diversity levels.

For non-endemic species (Figure S2), we did not run analyses of return to pre-human diversity because there are no recorded extinctions of native species that are not endemic to our focal region since human arrival. We also did not run analyses for the scenario where only threatened species go extinct, because none of the non-endemic species are classified as threatened. However, five non-endemic species are classified as near-threatened, and we thus ran analyses for the scenario where threatened and near-threatened species go extinct. Our model underestimates the number of non-endemic species and as such New Zealand would never recover on average to current diversity of non-endemic species because the plateau of the number of species is at a value below the actual current diversity.

DATA AND CODE AVAILABILITY

The maximum credibility trees from BEAST, underlying molecular matrices (alignments) are deposited in Mendeley Data: https://doi.org/10.17632/wj3xrjmj28.1. These include the GenBank accession numbers of the sequences downloaded for this study.

The DAISIE R objects for the different DAISIE analyses are deposited in Mendeley Data: https://doi.org/10.17632/5p3zf4wf3r.1.

New computer code was implemented in a new version of DAISIE R package available in: https://github.com/rsetienne/DAISIE.